

Rediscovery of the sacoglossan opisthobranch *Hermaea wrangeliae* (Ichikawa, 1993) in Okinawa, Japan

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Abstract: In December 2008, eight sacoglossan specimens of *Hermaea* Lovén, 1844 were collected from uniseriate red algae (cf. *Wrangelia tanegana*) at two sites on the west coast of Okinawa, Japan. These specimens are compared to the described *Aplysiopsis wrangeliae* Ichikawa, 1993 from Okinawa which we and other authors have previously suggested belongs to the genus *Hermaea*; we suggest that our specimens are attributable to *Hermaea wrangeliae* (Ichikawa, 1993).

Key words: Sacoglossa, Ascoglossa, *Aplysiopsis*, Rhodophyta, *Wrangelia*

Japan and Australia are two regions of high diversity for sacoglossan opisthobranchs, essentially “hot spots” compared to other geographic regions (Jensen 2007). Our work on Japanese shores (2002-2009) has supported Jensen’s biogeographic analysis. For example, our comprehensive synthesis of the literature (the indexed as well as the less accessible, non-indexed sacoglossan records) indicates that there are at least 100-150 species of sacoglossans on Japanese shores (Trowbridge *et al.* 2007 and unpubl. data).

Many western Pacific and Indo-Pacific species of sacoglossans are insufficiently described. This problem is acute for the cerata-bearing species (Limapontioidea), particularly those species associated with red algae. Trowbridge *et al.* (2009a) recently reviewed the approx. 20 species in three sacoglossan families that feed on red algae in the order Ceramiales; we concluded that the Okinawan species described as *Aplysiopsis wrangeliae* Ichikawa, 1993 undoubtedly belonged to the genus *Hermaea* Lovén, 1844. Because specimens were neither archived at Seto Marine Laboratory (contrary to Ichikawa 1993) nor retained by the author (M. Ichikawa, pers. comm.) and because no internal morphological features were described, it was not possible to confirm the correct genus. This was unfortunate because sabot-shaped radular teeth would largely support placement in the genus *Aplysiopsis* Deshayes, 1835. [The term sabot-shaped refers to that of a Dutch wooden shoe (Jensen 2001); within the family Hermaeidae, sabot-shaped teeth occur in *Aplysiopsis* but not in *Hermaea* (Jensen 1996)].

Based on the algal host association described for *Aplysiopsis wrangeliae* (namely the red alga *Wrangelia tayloriana*) and the fact that no *Aplysiopsis* species has been shown to feed preferentially on red algae pointed to Ichikawa’s species

belonging to *Hermaea*. Our interpretation (Trowbridge *et al.* 2009a) was implicitly supported by Jensen (2007) who also listed the Okinawan species as *Hermaea wrangeliae*.

After recently collecting eight sacoglossan specimens that appear to fit the description of *Aplysiopsis wrangeliae*, we investigated this issue more explicitly, considering nine characters that differ between the sacoglossan genera *Aplysiopsis* and *Hermaea* (Jensen 1996 and pers. comm.).

COLLECTIONS

On 11 December 2008, we collected five specimens of *Hermaea* from about 0.5 L of delicately branching red algae from the shallow subtidal region (<0.5 m deep) at Zanpami (26°26′15″N, 127°42′48″E) on the west coast of the main island of Okinawa, Japan. The algae grew profusely in dense turfs in sandy areas and as epiphytes on a variety of other macroalgae. The alga was uniseriate throughout (single row of cells attached end-to-end), diminutive (<5 cm tall), and extensively branched (Figs. 1H-M). N. Miyamoto, a phycologist resident in Okinawa, kindly confirmed the alga belonged to the order Ceramiales. The vegetative morphology was consistent with drawings by Okamura (1934) for *Wrangelia argus* (now considered to be *Wrangelia tanegana*). Non-reproductive algae, however, cannot be identified definitely to genus or species as most of the diagnostic traits relate to the temporally transient reproductive structures. Thus, we refer to the alga as cf. *Wrangelia*. Voucher specimens were made of this alga in case molecular identification might be possible.

The second collection was on 16 December 2008 at Sobe (26°23′12″N, 127°43′24″E) in Yomitan on the west coast

of the main island of Okinawa. We collected approx. 1.1 kg (wet weight) of the shallow subtidal green alga *Codium geppiorum* which often is covered in red algal epiphytes belonging to the Ceramiales. Although *C. geppiorum* has not previously been reported from Okinawa, Chang *et al.* (2002) recently redescribed the species complex and kindly identified our specimens in 2006 (J.-S. Chang, pers. comm.). While sorting through the *Codium*, we found three additional specimens of *Hermaea*. Because of logistic constraints (namely imminent departure from Okinawa), we did not have the opportunity to identify or characterize the red algal epiphytes.

DESCRIPTION AND DISCUSSION

External morphology

Type description

The holotype specimen—from Kuro Island, Okinawa—was 10 mm long (Ichikawa 1993); the length of the other five specimens was not provided. Key characters were auriculate rhinophores with a short ear-like flap and indented cerata containing digestive diverticulae. Other features included a transparent body, transverse stripes on rhinophores, white spots on the head, a large dark spot on the middle of the neck, and a white dotted line along the ventral border of the foot. There was a relatively schematic line drawing (Ichikawa 1993: fig. 3) and an out-of-focus photograph (plate II, fig. 11) to complete the half-page type description.

The assignment of Ichikawa's specimens to the genus *Aplysiopsis* was seemingly based on two attributes: auriculate rhinophores with a small flap and the presence of pale brown longitudinal lines on the sole of the foot of some (but not all) specimens. Based on Jensen (1996), such rhinophores are found in 2-3 genera: *Aplysiopsis*, *Hermaea*, and *Hermaeopsis* A. Costa, 1869 (the latter of which may be synonymous with *Hermaea*). They are also found in at least one *Costasiella* species, namely *Costasiella illa* (Marcus, 1965) (Jensen, pers. comm.). The second character is also problematic as it was found in only some individuals. No data were reported to evaluate the two other external characters that differ between the genera: the shape of the pericardium and the presence or absence of dorsal vessels (Table 1).

Our observations

Our Okinawan specimens ranged from 1.5 to 4.5 mm ($N = 8$). The auriculate rhinophores were distinctly grooved with a small flap; this character was readily observed at all angles (Figs. 1A-G). The specimens observed in detail had multiple transverse dark bands encircling the rhinophores. The intensity of the transverse markings varied considerably among specimens (Figs. 1A-G); the distal two bands were

more pronounced than the proximal band. Three transverse bands were distinct in our larger specimens. The regions between the bands were heavily encrusted with white pigment granules (Fig. 1C); thus, the dark bands appear dark in part because of the absence of white dots and in part because of the presence of dark pigmentation. Under low magnification, the dark color appeared black, but under high magnification, the spots appeared to be dark wine-colored to red in color on well-fed specimens (Figs. 1C-D). Dark pigment spots were not restricted to the rhinophore bands: they were also distributed sparsely between the longitudinal rows of cerata, the dorsal surface of the head, the lateral sides of the body, and the proximal surfaces of the cerata.

There were 8-12 large cerata per sacoglossan as well as 7-13 diminutive ones generally alternating with larger ones (Figs. 1A-B, Table 2). Cerata were covered with white spots, particularly on the distal ends, and contained digestive diverticulae approx. 100-150 μm in diameter. There was a central core with lateral primary branches that extended at an approx. 80-90° angle from the central core. The laterals extended out in typically 3-4 directions. In one specimen, the laterals also branched; in the other specimens, they did not.

The overall shape of the cerata within individuals was temporally changeable from mildly lumpy to extremely spiky. The ceratal surface could be contracted down to the diverticulae, at which point the widest part of each cerata was near the distal-most branches, rendering the cerata very knob-like. At other times (in the same individual slugs), the ceratal surface could be inflated or raised away from the relatively inflexible diverticulae; the difference in appearance between the contracted and expanded cerata was strikingly apparent. Ceratal shape, therefore, is not a strong diagnostic feature for species description.

The white spots described by Ichikawa (1993) were concentrated on the head, the tips of the cerata, rhinophores, and lateral margin of the foot. The spots are presumed to be pigment granules, not epidermal glands, as they did not release white fluid when the specimens were prodded with a blunt probe or gently squeezed with forceps. When we turned individual specimens over, the line of white dots demarcating the edge of the foot was distinctive. Most specimens lacked white dots on the ventral surface of the foot but all had the dots along the edge; one specimen had sparsely distributed dots across the sole that were not at all obvious.

In all specimens we observed (of this species and other *Hermaea* spp.), the anterior end of the digestive tract occurred posterior to the eyes as the esophagus extends dorsally and then veers to the left side of the animal. This section of the digestive system contains a large number of fresh, red algal chloroplasts; however, in well-fed specimens, the internal structure (esophageal pouch) clearly extends to the animal's left (Figs. 1A-G). We observed the entry of chloroplasts into

Table 1. Comparison of two sacoglossan genera based on 6 differences (from Jensen 1996) and 3 supplementary attributes.

Evidence	Characters (# ¹)	<i>Aplysiopsis</i>	<i>Hermaea</i>	<i>Aplysiopsis wrangeliae</i> ²	<i>Hermaea</i> sp. (this study)
Primary attributes					
	pericardium (20)	elongate	oval	not shown in drawing or photograph; not described in text	oval to round
	dorsal vessels (21)	present	absent	not shown in drawing or photograph; not described in text	none seen
	shape of radular teeth (32)	sabot-shaped	blade-shaped	not described	blade-shaped
	lateral flanges on teeth (35)	absent	present or variable ³	not described	unclear with light microscopy
	number of visceral ganglia (40)	3	2 ⁴	not described	2
	seminal receptacle (49)	absent	variable	not described	absent
Supplementary attributes					
	coloration	typically heavily pigmented	typically translucent	transparent ⁵	translucent
	sole of foot	pair of stripes present in many species	no stripes	pair of stripes in some specimens	no stripes
	algal diet	septate green algae (e.g., <i>Cladophora</i> or <i>Chaetomorpha</i>)	septate red algae (or diatoms in <i>Hermaea vancouverensis</i> O'Donoghue, 1924)	septate red alga <i>Wrangelia</i>	septate red algae

¹ character numbers based on Jensen (1996, table 3)² based on species description of Ichikawa (1993)³ depends on whether or not *Hermaea* and *Hermaeopsis* are considered synonymous⁴ this character is supported for our present species but not for two other Japanese *Hermaea* species we have dissected (Hirano *et al.*, unpubl. obs.)⁵ translucent is undoubtedly more appropriate

the esophageal pouch during feeding and the movement of chloroplasts and fluid into the digestive diverticulae.

Potential discrepancies

There were three apparent discrepancies between Ichikawa's description and our specimens. First, Ichikawa (1993) reported three green transverse bands on the rhinophores whereas we observed red ones. If the dark spots were colored by ingested algal chloroplasts (as is true with many sacoglossans), then the red vs. green color discrepancy presumably reflects variation in feeding status of the specimens: red algal chloroplasts turn green as they age and disintegrate.

Second, the dark spot on the middle of the neck illustrated by Ichikawa (1993: 126 in fig. 3) was posterior to the eyes and symmetrical. Our observations differed slightly from this description: the structure we saw (esophageal pouch) extends to the animal's left (Figs. 1A-G). Ichikawa's

photograph (plate II, fig. 11) appears consistent with ours (Fig. 1) despite the former being small and unfocused.

Third, Ichikawa (1993: 126) stated "Some of the paratype specimens have two light brown, longitudinal stripes on the sole of the foot, as in other species of *Aplysiopsis*". Such stripes occur in many Japanese species including *Aplysiopsis toyamana* (Baba, 1959), *Aplysiopsis minor* (Baba, 1959), and *Aplysiopsis orientalis* (Baba, 1949) but not *Aplysiopsis nigra* (Baba, 1949). We consider it rather inadequate to identify all specimens as *Aplysiopsis* based on a character found in only some individuals: genus determination should be based on characters in all conspecific specimens. None of our *Hermaea* specimens had such stripes. If Ichikawa's specimens were *Hermaea*, then how could we account for her observations? One possibility is that not all specimens have this trait, only some did. Another possibility is that she misinterpreted darker internal structures as superficial stripes. For example, the longitudinal trunks of the digestive

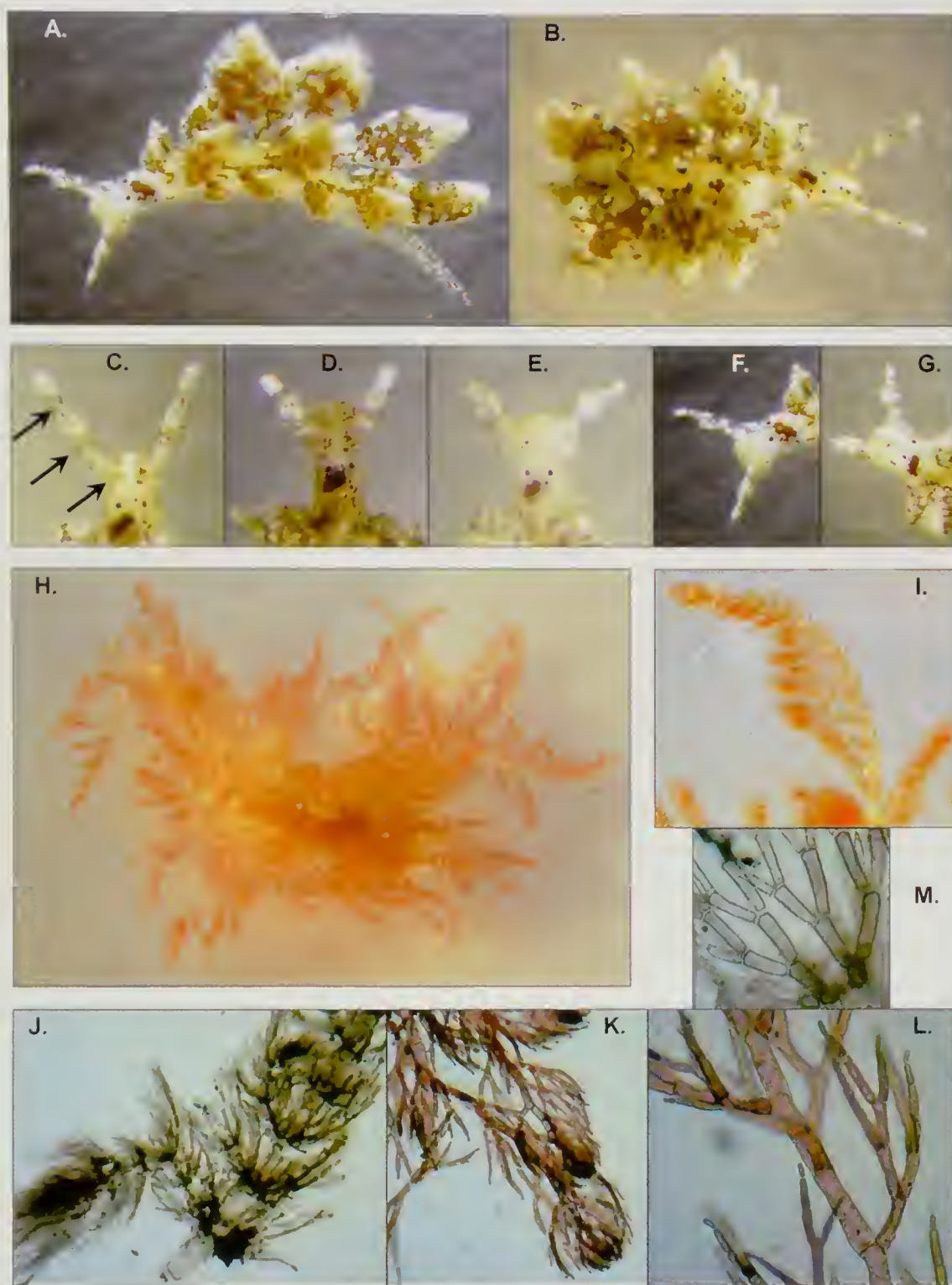


Figure 1. Specimens of *Hermaea wrangeliae* (Ichikawa, 1993) collected in December 2008 from two locations on the west coast of Okinawa, Japan. A-B, Oblique view of sacoglossan's side to illustrate the rhinophore shape, cerata attributes, presence of distinct esophageal pouch (pigmented by ingested red algal chloroplasts), and white pigment granules on rhinophores, cerata, tail, and elsewhere. C-G, Dorsal views of head with medial-lateral esophageal pouch (reddish brown structure). Transverse bands indicated by arrows in C; bands were less obvious in smaller specimens. Epidermal reddish-brown markings best seen in D. Specimens ranged in size from 1.5 to 4.5 mm long. H-L, Red algal host collected on 11 December 2008 from Zanpa-misaki, Okinawa. H, Entire thallus a few centimeters long; I, close-up of a single primary branch with lateral secondary branches. J, Close-up view of secondary branch, illustrating main axis with clusters of uniseriate branchlets arranged in whorls around the axis. K-M, Microscopic views of branchlets (ca. 100 μ m long and 15-20 μ m wide) with new branchlets arising at terminal ends of each cell. The sacoglossans puncture the cells of these branchlets.

diverticula (which contain chloroplasts) may be seen through the translucent sole of the foot. Variation in feeding (amount ingested and/or time since last meal) could cause variation in slug appearance.

Given the nature of Ichikawa's observations and descriptions of other sacoglossan species in the 1993 paper, we presume that our species is the one she described, but that the type description was superficial and rather stylized. A less parsimonious explanation (but not mutually exclusive) is that two or more sympatric *Hermaea* spp. feed on red algae in Okinawa.

Feeding and reproduction

Type description

Ichikawa (1993) reported *Aplysiopsis wrangeliae* from the red alga *Wrangelia tayloriana* (now considered synonymous with *Wrangelia tanegana* (see Guiry and Guiry 2009)). She stated that the sacoglossan species was "limited to" this alga, a rather strong statement given that she collected only six specimens and did not confirm actual feeding by the sacoglossan on the alga. She also stated that the body shape and color "perfectly match this host" (Ichikawa 1993: 126); the statement is potentially misleading as all or most *Hermaea* match their hosts, regardless of whether they are stenophagous or comparatively polyphagous on red algal hosts; the retention of ingested algal chloroplasts is the basis of this nutritional homochrony. Finally, no reproductive details were provided for this species.

Our observations

The specimens from Zanpa-misaki were collected from a Ceramialean red alga structurally similar to *Wrangelia tayloriana* (Figs. 1H-L). The uniseriate alga was a few centimeters long with delicately branching laterals that arose from the main axes in whorls at each node. The terminal branchlets (Figs.

Table 2. Details about 5 specimens of *Hermaea* collected from Zampa-misaki, western Okinawa on 11 December 2008.

Body length (mm)	# of cerata on left side	# of cerata on right side	Total # of cerata	Notes
3.5	4 large + 5 small	4 large + 2 small	15	• 2-3 tiers of primary branches on digestive diverticulae in cerata • no secondary branches
4.0	3 large + 8 small	6 large + 5 small	22	• 3-4 tiers of primary branches on digestive diverticulae in cerata • no secondary branches
4.0	5 large + 6 small	5 large + 6 small	22	• 3-4 tiers of primary branches on digestive diverticulae in cerata • only 1 secondary branch
3.0	6 large + 4 small	6 large + 5 small	21	• 3-4 tiers of primary branches on digestive diverticulae in cerata • no secondary branches
1.5	6 large + 4 small	4 large + 4 small	18	• not examined

1K-M) were approx. 100 μm long and 15-20 μm wide; these were the cells punctured and drained by our specimens. We confirmed the actual feeding of all our *Hermaea* specimens on the red alga (Figs. 1H-M). The slugs were strongly attracted to the algal thalli and punctured and emptied the uniseriate cells.

On 11 December 2008, we observed two of the specimens initiate direct frontal contact involving rubbing the frontal part of their heads together. This behavior was similar to that observed in *Stiliger berghi* Baba, 1937 directly before copulation and spawning. Although we did not observe the actual copulation, an egg mass was deposited within the next few hours and then another one on a subsequent day. There was one embryo per capsule and the masses lacked extra-capsular yolk. The timing of egg mass deposition did not enable us to measure uncleaved ova; we measured the capsules and embryos at the gastrula stage. Capsules averaged $106.3 \times 121.0 \mu\text{m}$ ($N = 15$) and embryos averaged $60.7 \times 67.9 \mu\text{m}$ ($N = 15$). These values are comparable to those of at least three other red algal feeders (*Hermaea bifida* (Montagu, 1815), *Stiliger fuscovittatus* Lance, 1962, and *Stiliger berghi*) (see Trowbridge *et al.* 2009a).

Internal anatomy

Type description

Ichikawa (1993) provided no details on internal anatomy of this species or of the other 11 new species described in the same publication. Thus, the four internal characters that could distinguish between *Aplysiopsis* and *Hermaea* (Table 1) could not be evaluated for the type specimen.

Our observations

We examined the radular morphology of two specimens to distinguish between *Aplysiopsis* (with sabot-shaped

teeth) and *Hermaea* (with blade-shaped teeth) (see Jensen 1996: 109). The buccal masses were removed from formalin-preserved specimens (fixed in 5% formalin seawater), placed in dilute bleach (10% Clorox) to remove organic tissue, and then examined and photographed under a compound microscope. The radular teeth were fairly thick (laterally) and blade-shaped, thereby refuting the *Aplysiopsis* placement.

The radula of the 3.5 mm specimen had 8 teeth plus 1 “ghost” tooth (forming) in the ascending series of unused teeth; the slug had 17 teeth plus 2-3 pre-radular elements (basal rod-like elements) and 3 transitional ones (with short, incompletely formed blades) in the descending series of used teeth. The leading tooth was 32.8 μm long and 12.5 μm wide at the base. The 4 mm specimen had 9 teeth plus 1-2 ghost teeth in the ascending series and 17 teeth plus 2-3 preradular elements and 3 transitional teeth in the descending series (Fig. 2). The size of the leading tooth was 34.3 μm long and 14.0 μm wide at the base. The cutting edge of each radular tooth appeared smooth under the light microscope. There was a lateral ridge on each tooth but whether this constituted “lateral flanges” (see Table 1) was unclear with light microscopy. In the two specimens examined, the descending series of teeth terminated in a loose coil of used teeth (see Fig. 2), not in tight ball nor in a heap of disarticulated teeth.

The pharynx was rather small. The pharyngeal lips were moderately thick, and the dorsal septate muscle was rather low and thin. The ventral ascus muscle was also thin and steeply inclined to the longitudinal axis of the pharynx. The esophagus was very short and had a rather large, elongate esophageal pouch immediately behind the nerve ring. In living specimens, the pouch is externally visible (Fig. 1) due to pigmented algal chloroplasts. The digestive tract then reached a small stomach from which a very short intestine ran to the

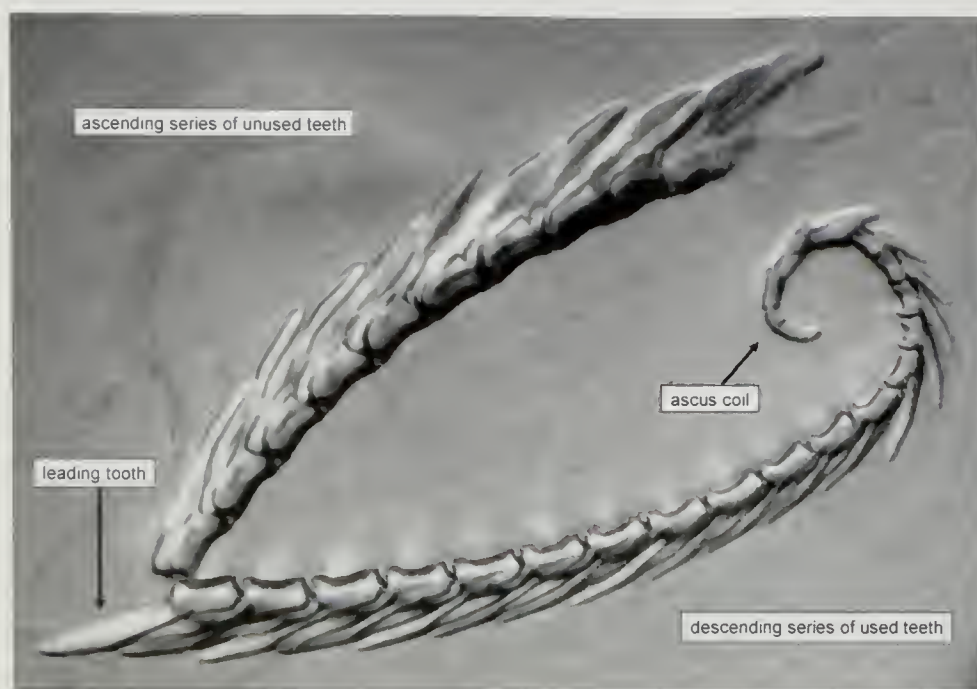


Figure 2. Radular ribbon of 4 mm specimen of *Hermaea wrangeliae* collected on 11 December 2008 from Zampa-misaki, Okinawa. Leading tooth was 34.3 μm long and 14.0 μm wide at base. Photographed under a compound light microscope.

anus which opened mid-dorsally and a little posterior to the esophageal pouch. Two main digestive gland tubules ran along the dorso-lateral surface of the body (Figs. 1A-B). The digestive diverticulae extended from these large tubules into the cerata (Fig. 1A).

Another important character determining whether or not a sacoglossan belongs to the genus *Hermaea* is a penis with no stylet (e.g., the superficially similar *Placida* Trinchese, 1876 has a stylet). Our dissection confirmed that the Okinawan specimens lack the stylet (i.e., unarmed penis) and had a diaulic reproductive system (two openings rather than three). In addition, two visceral nerve ganglia were seen (Table 1), indicating our specimens belong to *Hermaea*. (However, we have observed three visceral ganglia—rather than two—in two other Japanese *Hermaea* spp. so this might be a variable character at the genus level or earlier studies may have been less detailed).

The taxonomy of the cerata-bearing sacoglossans such as *Hermaea* has long been unstable and, in many respects, not well defined. Many species originally described as *Aplysiopsis* or *Hermaeopsis* were subsequently moved into the genus *Hermaea*, particularly due to blade-shape of radular teeth and red algal diet (see Table 1). Thus, the fact that our recorded Okinawan species, originally described as *Aplysiopsis wrangeliae*, actually belongs to *Hermaea* is not surprising. The proper name of this species consequently should be *Hermaea wrangeliae* (Ichikawa, 1993). Important external features include the transverse markings on the rhinophores, the sparse, club-shaped cerata, and the branched digestive diverticulae within the cerata.

A far more difficult question—and one largely beyond the scope of this paper—is the relationship of this described species and many other ones (described and undescribed species) around the world listed by Burn (2006), Gosliner *et al.* (2008), and Trowbridge *et al.* (2009a). The European *Hermaea bifida* and the Australian *Hermaea eveline-marcusae* Jensen, 1993 have been well described and the Japanese species is definitely not synonymous with either species; the distinct transverse markings on the rhinophores are lacking in these species. However, most of the congeners have not been well described. For example, the tooth shape is generally similar among many *Hermaea* species. The knob-like cerata with branching digestive diverticulae have been illustrated for many *Hermaea* spp. (e.g., Vogel 1971, Marcus 1972, Cervera *et al.* 1991). Yet, the branching patterns of digestive diverticulae are often highly stylized (as in Ichikawa 1993) so matching actual specimens to idealized illustrations is problematic; this issue is not limited to *Hermaea* but

plagues the descriptions of the majority of cerata-bearing sacoglossans. Comparisons of reproductive features of congeners are also problematic as the size of uncleaved ova, capsules, and larval shells have been reported in only a few cases such as the European *Hermaea bifida*, and reproductive anatomy has rarely been reported.

Basic natural history details, morphological information, and algal host associations are sorely needed for sacoglossan species, particularly the red algal feeders, in all geographic regions other than the North Atlantic Ocean. This report on an Okinawan *Hermaea* and related reports on other Japanese sacoglossans (Hirano *et al.* 2007a, 2007b, 2007c, 2008a, 2008b, Trowbridge *et al.* 2008a, 2008b, 2009a, 2009b) attempt to identify and characterize the sacoglossan fauna in a highly diverse but understudied geographic region with an amazing flora of potential algal hosts.

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